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## **Life History of Menhadens in the Eastern Gulf of Mexico**

WILLIAM R. TURNER

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WILLIAM R. TURNER

Bureau of Commercial Fisheries Biological Laboratory  
Beaufort, N. C. 28516

## ABSTRACT

Biological material collected with plankton and gill nets during cruises of the R/V *George M. Bowers* in the eastern Gulf of Mexico indicated that menhadens spawned principally near shore from November through March. Two species of menhaden—Gulf menhaden (*Brevoortia patronus*) and yellowfin menhaden (*B. smithi*)—and their hybrid abounded in collections during the winters of 1964 through 1967. Gulf menhaden, the most important commercial species, occurred throughout the study area but its numbers decreased to the east and south. Yellowfin menhaden were confined to the coastal region of peninsular Florida, whereas hybrids were taken only from Tampa Bay south to Cape Sable.

Hybrid menhaden apparently backcross freely with the parental species but the extremely high percentage of hybrid males ( $\geq 99\%$ ) assures against establishment of a hybrid population. The likelihood of natural hybridization and introgression was substantiated by artificial fertilization experiments.

In addition to the menhadens, six other clupeids entered the combined collections. Three of these species—Atlantic thread herring (*Opisthonema oglinum*), scaled sardine (*Harengula pensacolata*), and Atlantic round herring (*Etrumeus teres*)—have spawning seasons that coincide, in part, with that of the menhadens. The early life stages of these species, although undescribed, were probably represented in the plankton collections.

## INTRODUCTION

Of the three species of menhaden found in the Gulf of Mexico, the Gulf menhaden, *Brevoortia patronus*, is by far the most important commercially. Species of lesser importance are the yellowfin menhaden, *B. smithi*, and the finescale menhaden, *B. gunteri*. Menhaden are exploited commercially in coastal waters of the northern Gulf chiefly from April through September. Generally, menhaden schools are no longer available to purse-seiners by the end of October; presumably the fish have migrated to offshore spawning areas. Although several accounts have been published of eggs and larvae of menhadens collected off the Atlantic coast (Kuntz and Radcliffe, 1917; Reintjes, 1961, 1962; Massmann, Norcross, and Joseph, 1962; and others), eggs of the Gulf menhaden have never been described.

During the winters of 1964–65, 1965–66, and 1966–67, personnel of the Bureau of Commercial Fisheries Exploratory Fishing and Gear Research Base at Pascagoula, Mississippi, conducted monthly cruises aboard the R/V *George M. Bowers* to determine the distribution of clupeids in the eastern Gulf. Since Gulf menhaden spawn principally during fall and winter, as inferred from dates of entrance of the larvae into estuaries (Sutt-

kus, 1956; Springer and Woodburn, 1960), the cruises afforded an opportunity to obtain biological material for life history studies. Staff biologists from the Bureau's Biological Laboratory in Beaufort, North Carolina, participated in 11 cruises to study the temporal and areal distribution of adult and early stage menhaden.

## METHODS

*Sampling Locations.*—In 1964–65, sampling stations were occupied at 43 locations between Panama City and Cedar Keys, Florida, and in 1965–66, stations were occupied at 48 locations from Cedar Keys to Cape Sable, Florida (Figure 1). The Florida cruises provided coverage offshore to the 32-fathom contour. In 1966–67, stations were occupied at 22 locations in the area between Chandeleur Island, Louisiana, and the offing of Mobile Bay, Alabama, mainly in Mississippi Sound. Since samples in each area were obtained in different years, it was assumed that seasonal changes in each area closely follow the same pattern from year to year.

Fishing locations varied on each cruise, depending on the distribution of fish schools. Fish schools were usually located by aerial surveys during the week preceding a cruise, and subsequent netting was concentrated in

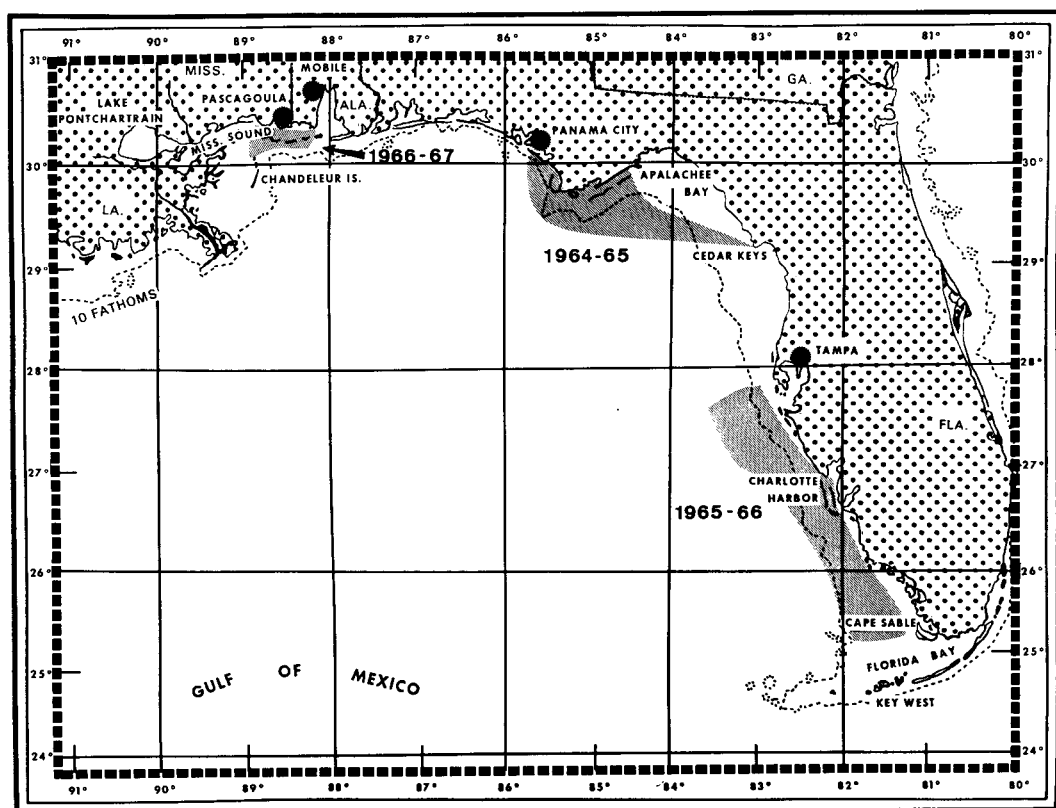


FIGURE 1.—Eastern Gulf of Mexico. Shaded regions represent areas where menhaden material was collected.

the areas where schools had been spotted. During the cruises, schools were relocated either by sight or by echo tracings on a fathometer. The 1966-67 cruises were not preceded by aerial surveys.

**Sampling Gear.**—Menhaden material was obtained by fishing gill nets from surface to bottom and by towing plankton nets just below the surface in waters ranging from 1 to 32 fathoms deep. Gill nets, consisting of a series of 300- by 10-foot shackles of monofilament mesh grading from 1-3/8 to 3-1/4 inches, stretched measure, were fished obliquely from surface to bottom. Usually, 8 to 10 shackles were fished at each location, but the amount of net and fishing time varied considerably. Most of the fishing was inside the 5-fathom contour. In Mississippi Sound only two panels (2- and 2-5/8-inch mesh) were fished at each gill-net station.

While the gill nets fished, a 1/2-meter plankton net (mesh aperture equivalent to Number 0 silk) was towed nearby for 30 minutes at a speed of 2 to 4 knots. Occasionally, the plankton net was towed between fishing locations; the duration of these tows varied from 10 minutes to 1 hour. All plankton samples were preserved in 5% formalin buffered with borax.

**Treatment and Identification of Material.**—Menhaden taken in gill nets were examined immediately to determine the stage of sexual maturity, and artificial fertilizations were attempted with fish in the most advanced stage of development. Ova were stripped into finger bowls and mixed with sperm. Sea water, filtered to remove foreign matter, was added and the eggs were checked periodically for development. The eggs of most clupeids taken during the cruises were too green for success-

TABLE 1.—Menhaden eggs and larvae taken in plankton samples from three areas of the eastern Gulf of Mexico

Month	Northern Florida (1964-65)					Southern Florida (1965-66)					Mississippi Sound (1966-67)				
	Collection dates (inclusive)	Tow time (minutes)	Number of eggs	Larvae		Collection dates (inclusive)	Tow time (minutes)	Number of eggs	Larvae		Collection dates (inclusive)	Tow time (minutes)	Number of eggs	Larvae	
				Number	Length range (mm)				Number	Length range (mm)				Number	Length range (mm)
Oct.	—	—	—	—	—	—	—	—	—	—	10-14	90	0	0	—
Nov.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dec.	9-15	300	28	4	11-14	—	—	—	—	—	12-15	385	23	46	8-18
Jan.	4-9	390	173	4	11-17	18-23	500	155	247	7-20	11-13	210	8	21	6-22
Feb.	3-6	180	0	7	15-18	21-27	430	4,376	73	5-20	—	—	—	—	—
Mar.	18-23	300	5	104	7-23	15-21	295	0	28	11-15	—	—	—	—	—
Apr.	—	—	—	—	—	7-9	210	0	10	11-15	—	—	—	—	—
Total	—	1,170	206	119	7-23	—	1,435	4,531	358	5-20	—	685	31	67	6-22

ful fertilization, although on one cruise a single ripe female yellowfin menhaden provided three different developmental series. These series were subsequently used to identify menhaden eggs in plankton collections. Representative samples of all clupeids taken in the gill nets were preserved in 10% formalin and, along with the plankton samples, brought to the laboratory at Beaufort for examination.

Gulf menhaden eggs have never been described, but they probably resemble those of other menhadens. Menhaden eggs collected during the cruises of *George M. Bowers*, therefore, were tentatively identified by their similarity to described eggs. Reintjes (1962) obtained a developmental series of yellowfin menhaden eggs and yolk sac larvae from the Atlantic coast of Florida through artificial fertilization. Hettler (1968) secured mature eggs from a yellowfin menhaden off the Gulf coast of Florida and duplicated this achievement. Hettler also cross-fertilized eggs from this fish with the milt of Gulf menhaden, to give hybrid eggs of known origin, *B. smithi* × *B. patronus*. Lastly, eggs from the same yellowfin menhaden were fertilized with sperm from a natural menhaden hybrid to obtain a backcrossed series. Developing eggs from the three separate fertilizations were indistinguishable (Hettler, 1968). Both Hettler and Reintjes were able to rear the eggs through hatching, but the larvae died soon after yolk sac absorption.

Menhaden larvae in the plankton collections were primarily distinguished by characters outlined by Suttkus (1956), who described the larval development of Gulf menhaden (18.9 mm standard length and above) from Lake Pontchartrain, Louisiana.

#### DISTRIBUTION OF EGGS AND LARVAE

Material in the plankton collections indicated that menhaden spawning in the Gulf off northern and southern peninsular Florida reached a peak in January and February (Table 1). Menhaden eggs were detected in the northern Florida samples from December 1964 through March 1965, and the collection of larvae 11 to 14 mm fork length in early December suggested that some fish had spawned in November. (No samples were obtained in November.) In the southern area sampling did not begin until January 1966, when spawning was already underway. The collection of 11 to 15 mm larvae in April indicated that menhaden spawned well into March even though no eggs were obtained that month.

The fact that all menhaden eggs and larvae were taken within the 10-fathom contour (most within the 5-fathom curve) suggests spawning takes place near shore in Florida waters. Plankton samples from outside the 10-fathom contour at seven locations did not contain menhaden eggs or larvae. Eggs and larvae were not taken more than 15 miles offshore, and the greatest concentration was within Charlotte Harbor in the southern area. Generally, menhaden eggs and larvae were more abundant off southern Florida than off northern Florida.

In Mississippi Sound and adjacent waters, menhaden eggs and larvae were taken during the December and January cruises. As in northern Florida, the collection of large larvae (18 mm) by mid-December indicated that menhaden spawned at least as early as November. The absence of eggs and larvae in

TABLE 2.—Number of adult menhaden caught with gill nets in three areas of the eastern Gulf of Mexico

Month	Northern Florida (1964-65)				Southern Florida (1965-66)				Mississippi Sound (1966-67)			
	Number of shackle-hours	Gulf men-haden	Yellow-fin men-haden	Hybrid men-haden	Number of shackle-hours	Gulf men-haden	Yellow-fin men-haden	Hybrid men-haden	Number of shackle-hours	Gulf men-haden	Yellow-fin men-haden	Hybrid men-haden
Oct.	—	—	—	—	—	—	—	—	3	266	0	0
Nov.	—	—	—	—	—	—	—	—	—	—	—	—
Dec.	114	323	6	0	—	—	—	—	7	182	0	0
Jan.	88	468	0	0	202	23	464	147	7	5	0	0
Feb.	66	84	0	0	156	35	321	216	—	—	—	—
Mar.	189	835	101	0	135	64	108	259	—	—	—	—
Apr.	—	—	—	—	131	2	89	25	—	—	—	—
Total	457	1,710	107	0	624	124	982	647	17	453	0	0

October samples did not preclude earlier spawning, as no offshore stations were occupied during that cruise. Suttkus (1956) found Gulf menhaden larvae entering Lake Pontchartrain in December and presumed that spawning began in October.

Surface-water temperatures at stations yielding eggs and larvae varied from 11 C in February to 18 C in March off northern Florida, and from 16 C in January to 23 C in March off southern Florida. Surface waters of Mississippi Sound were cooler; the temperatures ranged from 10 C in January to 15 C in December. Surface salinity at the plankton stations ranged from 33‰ in March to about 35‰ in January off southern Florida. Salinity was more variable in Mississippi Sound where it ranged from 25 to 32‰ in December. Salinities were not recorded for northern Florida waters.

Other clupeiform larvae closely resembling menhaden appeared in the March and April collections off southern Florida. These larvae, separated from menhaden by development of maxillary serrae, relative positions of the dorsal and anal fins, and general body conformation, were provisionally assigned to the genera *Opisthonema* and *Harengula* (John W. Reintjes, pers. comm.). Springer and Woodburn (1960) indicated that the scaled sardine, *Harengula pensacolae*, spawns during April and May in the area of Tampa Bay, Florida, and Hildebrand (1963) stated that the Atlantic thread herring, *Opisthonema oglinum*, spawns during May and June in the vicinity of Beaufort, North Carolina. Ripe males and nearly ripe females of both species were taken on March 15 during the 1966

cruises of the *George M. Bowers* in the warmer waters 25 miles NNE of Key West, Florida. Artificial fertilization attempted with the most advanced individuals was unsuccessful. Conceivably, the undescribed early stages of these species could occur in this area together with those of menhaden.

#### DISTRIBUTION AND MATURITY OF ADULTS

Gulf menhaden, yellowfin menhaden, and their hybrid were taken during the cruises (Table 2). Only Gulf menhaden were caught in Mississippi Sound, whereas Gulf and yellowfin menhaden were caught off northern Florida. Both species and their hybrid were taken off southern Florida. Gulf menhaden constituted 94% of the total menhaden catch off northern Florida but only 7% of the catch off southern Florida. Conversely, yellowfin menhaden dominated the catch off southern Florida (56%); hybrids made up the remaining 37% of the catch from this area.

The sample distributions of adult menhaden paralleled those of eggs and larvae along the Florida coast; all menhaden were collected within the 10-fathom contour. Gill nets fished at eight locations in deeper water (10 to 32 fathoms) failed to catch menhaden. Roithmayr and Waller (1963) reported winter concentrations of menhaden in northern Gulf waters 4 to 48 fathoms deep and concluded that menhaden did not stray far from summer fishing grounds. The present studies indicated even less offshore movement along the Florida coast.

Approximately 3,500 menhaden taken during the cruises were examined to determine the stage of gonad development. Stages of

maturity currently used for menhaden were modified from a general classification outlined by Kesteven (1960), and were based on the following macroscopic characters:

Stage I—*Immature*: Virgin gonads, very small; ovaries torpedo-shaped, deep red, eggs invisible; testes thin, knife-shaped, whitish or grayish red.

Stage II—*Maturing virgin or recovering spent*: Ovaries red to yellow, occupying about one-third to one-half of the body cavity, eggs invisible; testes swollen but still thin, white or gray.

Stage III—*Ripening*: Gonads swollen, occupying about two-thirds of body cavity; ovaries yellow, opaque eggs visible through ovarian membrane; testes with white milt.

Stage IV—*Ripe*: Gonads occupying three-fourths or more of body cavity; ovaries yellow with opaque and some translucent eggs; milt and eggs sometimes extruded under pressure.

Stage V—*Spent*: Gonads shrunken, blood-shot, and flaccid; ovaries red to yellow, some residual eggs in lumina; testes similar to Stage II.

More than 1,500 Gulf menhaden taken off northern Florida in 1964-65 were examined for stage of sexual maturity. Most of the ovaries examined from December through February were classified as Stage III—*Ripening*; none had advanced to the ripe condition (Stage IV). Stage-IV males were generally available throughout this period, but were far less common than Stage III. By March, most menhaden were either spent (Stage V) or in a recovering condition (Stage II).

Only six yellowfin menhaden (Stage III) were taken in the December catches off northern Florida, and none was taken during the peak spawning months, January and February. The entrance of spent yellowfin menhaden into the catch in greater numbers (101) in March suggests a southward movement of this species during the spawning season. Young-of-the-year yellowfin menhaden have been collected in Tampa Bay (Springer and Woodburn, 1960), but have not been recorded from more northerly nursery areas.

Over 1,500 menhaden from southern Florida were also examined for stage of maturity. A small number of ripe (Stage IV) female

yellowfin menhaden were encountered in February and March, whereas ripe males of both species and their hybrid were available throughout the cruise period, January-April. Ripe menhaden taken in the March collections were used to obtain the series of artificial fertilizations referred to previously.

Approximately 400 Gulf menhaden from Mississippi Sound were examined for stage of maturity. None of the fish examined was ripe, but many in the December and January collections were categorized as advanced Stage III. Artificial fertilizations attempted with these fish were unsuccessful.

#### HYBRIDIZATION

Records of hybridization among clupeids are rare. Reintjes (1960) mentioned the possible occurrence of hybrid menhaden along the Atlantic coast of Florida. Later, Dahlberg (1966) gave a systematic account of this hybrid (*B. tyrannus* × *B. smithi*) from the Indian River and also described another hybrid (*B. patronus* × *B. smithi*) from the Gulf coast of Florida. A cross between the Gulf menhaden and the finescale menhaden (*B. gunteri*) from the western Gulf has not been reported.

Although hybrid menhaden have been reported along the Gulf coast of Florida from Apalachee Bay south to Florida Bay (Dahlberg, 1966), none was taken in the *George M. Bowers* collections north of Cedar Keys. The Gulf coast of Florida represents a region of overlap in the ranges of the Gulf menhaden (which becomes scarce to the south) and the yellowfin menhaden (which becomes scarce to the north). Numerical imbalance between the two parent populations favors hybridization, the less abundant species joining spawning aggregations of the predominant species. Hubbs (1961) stated that unequal numbers help break down isolating mechanisms between many freshwater species. This imbalance was also recognized by Minckley and Krumholz (1960) as contributing to the hybridization of threadfin and gizzard shad in the Ohio River, the only record of natural hybridization among freshwater clupeids in North America.

*Morphology*.—The separation of hybrids of Gulf and yellowfin menhaden from the

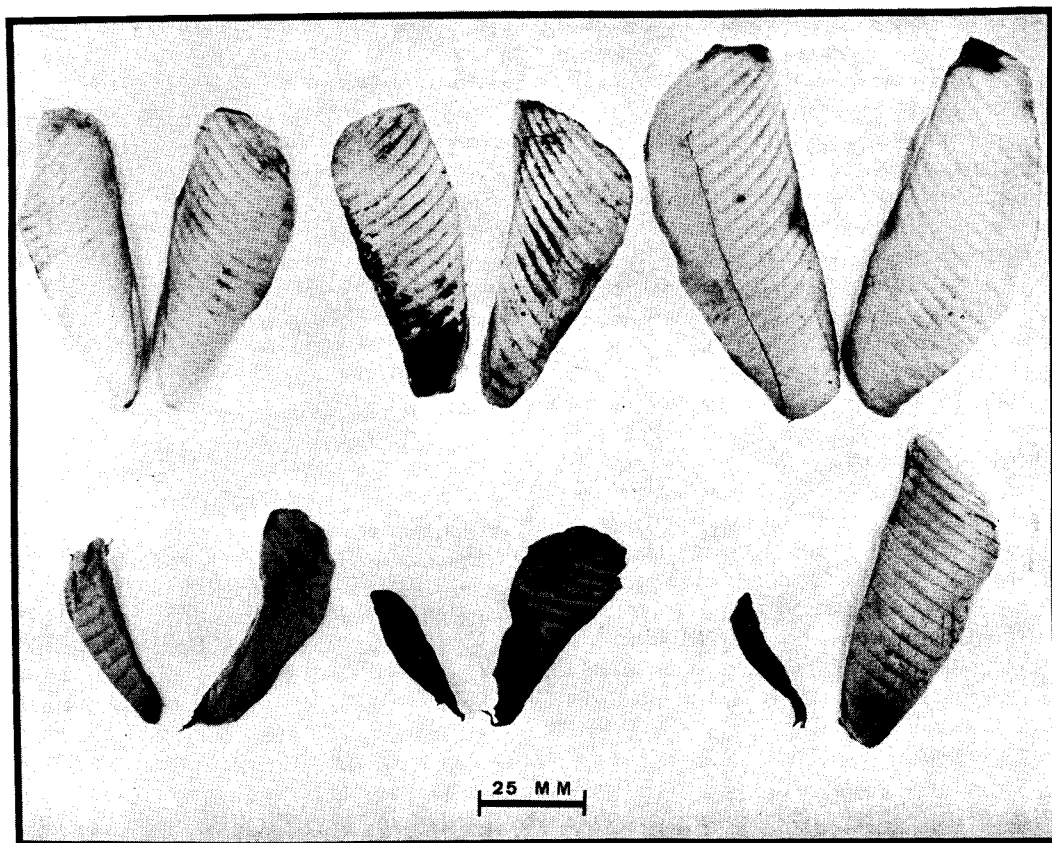


FIGURE 2.—Symmetrical testes (upper row) of Gulf menhaden from Mississippi Sound. Asymmetrical testes (lower row) of hybrid menhaden (*B. patronus* X *B. smithi*) from southern Florida.

parental species in the southern Florida samples was arbitrarily based on the degree of intermediacy of morphological characters. The development of opercular striae and the frontal groove, number of pre-dorsal scales, shape of the pelvic fins, and distribution and number of lateral spots were regarded as the most reliable distinguishing characters (Dahlberg, 1966). Hybrid menhaden apparently are fertile and, as a result of backcrossing, the offspring structurally grade into the parent species. This blending of characters through backcrossing compounded by an initially low degree of systematic divergence between the parents, makes positive identification of all specimens virtually impossible. The backcrossing accomplished by Hettler (1968) verified experimentally the viability of hybrid gametes.

Hybrids were perhaps best characterized

by asymmetrical testes (Figure 2). The development of one testis, on either side, was greatly reduced in hybrids, whereas disparity in the size of the testes was much less pronounced in the presumably pure strain menhadens. Because of introgression, however, all gradations existed between hybrids and the parental species. To differentiate the morphology of the hybrids and the parental forms, I compared the testes in allopatric samples of Gulf menhaden from Mississippi Sound and hybrids from southern Florida. The menhaden from Mississippi Sound assure, as much as possible, against the influence of hybridization. Mean differences between the weights of the left and right testes from fish of the same stage of development (Stage III) were 0.5 gram for Gulf menhaden and 4.1 grams for hybrids. These differences did not vary with fish size. A test between the means

of the two samples showed these differences to be highly significant ( $t = 6.37$ ;  $t_{.01} = 2.68$ ). Yellowfin menhaden from outside the area of hybridization were not available for examination, but were assumed to have symmetrical testes.

**Sex Ratios.**—Collections of hybrid menhaden were further characterized by a preponderance of males; only 4 of 390 hybrids were females. The presence of unbalanced sex ratios in the parental species in the samples from southern Florida suggests that they were affected by introgression. Of 540 menhaden identified as yellowfin menhaden, 346 were males and 194 were females. Fifty-two of 68 Gulf menhaden were males. The predominance of males in the collections was apparently unrelated to gear selectivity, as gill nets with the smallest and largest meshes rarely caught menhaden. Nonselection of sexes by the nets was also corroborated by the lengths of menhaden in the catch.

An unbalanced sex ratio and dominance by males characterizes many interspecific hybrids. Childers and Bennett (1961) found a high percentage of males (97-100%) among certain hybrid combinations of sunfishes, genus *Lepomis*, and, when such imbalance existed, an  $F_2$  generation was not produced. The lack of reproduction was not attributed to an absence of females, but to incompatible mating behavior between  $F_1$  males and females. Although the high percentage of  $F_1$  male menhaden obviously would greatly reduce the probability of producing an  $F_2$  generation, behavioral and physiological blocks may likewise serve as effective isolating mechanisms.

A preponderance of female Gulf menhaden entered catches in the northern areas. Of 1,641 Gulf menhaden from northern Florida, 1,085 were females (56 of 107 yellowfin menhaden from this region were females). Of 387 Gulf menhaden from Mississippi Sound, 224 were females and 163 were males. The reason for such unbalanced sex ratios apparently was not gear selectivity. The premise of non-selectivity by the nets was supported by the lengths of fishes captured; male Gulf menhaden ranged from 115 to 243 mm fork length and averaged 183 mm, whereas fe-

males ranged from 117 to 237 mm and averaged 190 mm. Such ratios imply sexual segregation during the spawning season, however samples from commercial landings during the summer in the eastern Gulf also have yielded rather erratic sex ratios from year to year. Females made up 61% of the landings in the eastern Gulf in 1964, whereas in 1965 and 1966 the sexes were almost evenly divided (Bureau of Commercial Fisheries, unpublished data).

#### ASSOCIATED CLUPEIDS

The Atlantic thread herring was the most numerous clupeid in the combined catches from all three areas and was followed in order of decreasing abundance by the menhadens, scaled sardine, Spanish sardine (*Sardinella anchovia*), Alabama shad (*Alosa alabamiae*), skipjack herring (*A. chrysochloris*), and Atlantic round herring (*Etrumeus teres*). Thread herring, scaled sardine, and Spanish sardine were most common in catches from southern Florida, whereas *Etrumeus* and both species of *Alosa* were confined to the northern samples. Besides Gulf menhaden, Alabama shad was the only other clupeid taken by gill nets in Mississippi Sound, although thread herring and scaled sardines were taken in the same region by sampling at night with different gear.

Adult thread herring and scaled sardines abounded off the coast of southern Florida from January through April in 1966, but were not taken in gill nets set off northern Florida or in Mississippi Sound during corresponding months of 1965 and 1967. A few young of these species, however, were collected by experimental purse seines fished in Mississippi Sound during October 1966. The smallest specimens were 40 mm long (fork length) and ranged upwards to 102 mm. Apparently the adults move southward along the coast or offshore during the winter as neither species was taken by gill nets fished in the northern Gulf from December through March. Ripe males and ripening females of both species were caught near the surface in 8 fathoms of water 25 miles NNE of Key West, Florida on March 15 (Table 3).

Alabama shad and skipjack herring were

TABLE 3.—Distribution and maturation stages of clupeids other than menhaden caught by gill nets in the eastern Gulf of Mexico

Species and area	Year	Number captured							Total	Gonadal stages represented
		Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.		
<i>Alosa alabamiae</i>										
Mississippi Sound	1966-67	0	—	13	3	—	—	—	16	II
Northern Florida	1964-65	—	—	15	0	5	10	—	30	II
Southern Florida	1965-66	—	—	—	0	0	0	0	0	
<i>A. chrysochloris</i>										
Mississippi Sound	1966-67	0	—	0	0	—	—	—	0	
Northern Florida	1964-65	—	—	0	0	10	4	—	14	II
Southern Florida	1965-66	—	—	—	0	0	0	0	0	
<i>Etrumeus teres</i>										
Mississippi Sound	1966-67	0	—	0	0	—	—	—	0	
Northern Florida	1964-65	—	—	3	0	10	0	—	13	not examined
Southern Florida	1965-66	—	—	—	0	0	0	0	0	
<i>Harengula pensacolatae</i>										
Mississippi Sound	1966-67	11	—	0	0	—	—	—	11	I
Northern Florida	1964-65	—	—	0	0	0	0	—	0	
Southern Florida	1965-66	—	—	—	59	142	157	210	568	III, IV
<i>Opisthonema oglinum</i>										
Mississippi Sound	1966-67	5	—	0	0	—	—	—	5	I
Northern Florida	1964-65	—	—	0	0	0	0	—	0	
Southern Florida	1965-66	—	—	—	1,902	251	1,140	2,188	5,481	III, IV
<i>Sardinella anchovia</i>										
Mississippi Sound	1966-67	0	—	0	0	—	—	—	0	
Northern Florida	1964-65	—	—	9	23	4	0	—	36	II
Southern Florida	1965-66	—	—	—	19	83	0	76	178	II

observed from December through March in the northern Gulf. According to Laurence and Yerger (1967) the Alabama shad is the most abundant anadromous fish on the Gulf coast of Florida and spawns in tributaries to Apalachee Bay from February to April. The spawning habits of the skipjack herring are still largely unknown. Specimens taken during the present studies ranged from 220 to 280 mm long and possessed immature gonads.

Small numbers of Atlantic round herring entered catches off northern Florida in December and February, but the condition of their gonads was not recorded. This species reportedly spawns during the winter in the northern Gulf (Hildebrand, 1963), thereby overlapping the menhaden spawning season in that area. Atlantic round herring larvae were described by Hildebrand (1963), but the eggs of this species are still undescribed (Mansueti and Hardy, 1967).

Adult Spanish sardines were taken off northern Florida from December through February and off southern Florida from January through April. Juveniles about 60 mm long were collected by dip nets under attractant lights at night off southern Florida in January.

#### SUMMARY

The collection of early life stages of menhaden in the eastern Gulf of Mexico indicated that spawning occurs principally near shore from December through March. The size of larvae in early December collections indicated that some spawning takes place in November. The condition of gonads in menhaden taken with gill nets also substantiates this spawning time. Although ripe males were taken in gill nets from December to March, ripe females were scarce. Ovaries of most menhaden examined during this period were ripening (Stage III); a few ripe female yellowfin menhaden were caught off southern Florida in February and March. Spent menhaden were collected in March and April.

Two species of menhaden—Gulf menhaden and yellowfin menhaden—and their hybrid entered the catch from the eastern Gulf. Only Gulf menhaden were collected from Mississippi Sound; Gulf and yellowfin menhaden off northern Florida; and both species and their hybrid off Florida south of Tampa Bay. Conditions favoring hybridization, however, exist all along the Florida peninsula where two sympatric species of menhaden occur in

numerical imbalance. The Gulf menhaden decreased in numbers as the yellowfin menhaden increased to the east and south.

Gulf and yellowfin menhaden are very closely related; hence differences in most morphological characters are slight. Interbreeding and backcrossing, coupled with this low degree of systematic divergence, makes recognition of hybrids difficult. The hybrids and the parent species differed most with respect to the size of the testes. In the hybrids one testis was reduced and the other was normally developed, whereas in the parent species the testes were developed symmetrically. Differences in the mean weights of the large and small testes of hybrids were highly significant. A broad spectrum of variation in testis development existed between the hybrids and the parent species, however, which strongly suggests introgression. Gametic compatibility between the two species of menhaden and also between the hybrid and the yellowfin menhaden was artificially demonstrated.

A predominance of males further characterized the hybrids; only 4 of 390 hybrids examined were females. This preponderance of males undoubtedly limits the reproductive success of the  $F_1$  generation but behavioral and physiological blocks may also prevent the perpetuation of a hybrid population. Although unbalanced sex ratios also characterized non-hybrid menhaden populations, females generally dominated.

Six other clupeids were associated with menhadens in the fish collections. Ranked in order of decreasing abundance they were: Atlantic thread herring, scaled sardine, Spanish sardine, Alabama shad, skipjack herring, and Atlantic round herring. Gonad development in two of these species, the Atlantic thread herring and scaled sardine, indicated that their spawning season partially coincides with that of menhadens off southern Florida. The early stages of these species, as well as the eggs of Atlantic round herring, have never been described and it is likely that they resemble those of menhaden.

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